TEUTHOPHAGOUS PREDATORS AS COLLECTORS OF OCEANIC CEPHALOPODS: THE CASE OF THE ADRIATIC SEA

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Abstract: Adults and subadults of pelagic cephalopods are quite elusive of man-made sampling devices. On the contrary, many cephalopod predators appear to be efficient collectors of the pelagic teuthofauna. Valuable data on the pelagic assemblage of the South Adriatic were gathered through the examination of the stomach contents of six teuthophagous predators, namely the cetacean Grampus griseus (Risso's dolphin), the bony fish Xiphias gladius (swordfish), and the chondrichthyans Prionace glauca (blue shark), Scyliorhinus canicula (smallspotted catshark), Galeus melastomus (blackmouth catshark), and Etmopterus spinax (velvet belly). In the stomach contents, 18 species of oceanic cephalopods were found, six of which had not been reported in the Adriatic until a decade ago. Several species previously unrecorded or otherwise considered rare were found to be fairly common or even abundant. Due to the selectivity of each different predator, the feeding spectra of the six predators give a biased representation of the actual situation of the cephalopod assemblage. Nevertheless, a completely new overall picture was obtained through predatortrician studies: the Adriatic assemblage of pelagic cephalopods is quite diverse and many items of it are rather common and abundant.

Riassunto: I predatori teutofagi come strumento di cattura di cefalopodi pelagici: il caso dell'Adriatico. Gli adulti e subadulti dei cefalopodi pelagici eludono ampiamente gli strumenti di cattura costruiti dall'uomo. Di contro, diversi predatori riescono a "campionare" efficacemente la teutofauna pelagica. Grazie all'esame dei contenuti gastrici di sei predatori teutofagi provenienti dall'Adriatico meridionale –il cetaceo Grampus griseus (grampo), il teleosteo Xiphias gladius (pesce spada), i condritti Prionace glauca (verdesca), Scyliorhinus canicula (gattuccio), Galeus melastomus (boccanera) ed Etmopterus spinax (sagrì nero)– si sono acquisite importanti informazioni sull'insieme dei cefalopodi pelagici di questo mare. Negli stomaci sono state rinvenute 18 specie di cefalopodi oceanici, sei delle quali non erano state segnalate per l'Adriatico fino ad una decina d'anni fa. Diverse specie, non registrate in precedenza o comunque ritenute rare, sono risultate piuttosto comuni ed abbondanti. La rappresentazione della situazione reale della teutofauna adriatica, fornita dagli spettri alimentari dei sei predatori, è viziata dalla selettivitià dei singoli predatori. Ciò non di meno, per mezzo degli studi sui predatori, si è ottenuto un quadro complessivo del tutto nuovo: la teutofauna pelagica dell'Adriatico presenta una rilevante diversità, con molti elementi piuttosto comuni ed abbondanti.

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Introduction

The assessment of the structure of oceanic communities is strongly hindered by the selectivity of sampling gear (Barkley, 1972). The severe limitations in collecting pelagic cephalopods by nets have been pointed out by Roper (1977), Clarke (1977), and Wormuth & Roper (1983). In general, different types of net capture different assemblages of cephalopods in terms of both number of species and specimens per unit of volume of filtered water. What is most obvious is how the size of the caught cephalopods increases with the surface increase of the mouth opening of nets (Roper, 1977). The examination of samples collected by the customarily used midwater trawls, such as the 3 m Isaacs-Kidd Midwater Trawl, gives the

impression that subadults and adults of several cephalopods are extremely rare, whereas the early juveniles and juveniles of the same species are much more abundant.

Indeed, the examination of stomach contents of teuthophagous predators has shown that the adults of many pelagic cephalopods are not as rare as supposed (Clarke, 1977). For instance, the juvenile stages of *Ancistrocheirus lesueurii* (known as *Thelidioteuthis alessandrinii*; *cf.* Bello, 1992a) have been collected in large quantities by plankton and midwater nets in all the oceans of the world (*cf.* Clarke, 1966 and Piatkowski & Welsch, 1991), whereas only three adults have been collected directly from the sea: the first one floating dead on the surface, the second by net, the third by squid jig (Bello *et al.*, 1994). Several adult specimens, however, have been found in the stomach contents of predators, such as sperm whales (Clarke, 1980). The holotype of the species itself was retrieved from the stomach of a dolphin (*cf.* Bello, 1992a). In general terms, Clarke (1966) states "Many species of squid which are important in the diet of predators are rarely, if ever, caught by man-made collecting devices"; Voss (1967) points out that "many species are known only from the stomach of predators."

In recent times a forward impulse in the study of cephalopods as prey was provided by the seminal work of Malcolm Clarke on their mandibles or "beaks" (e.g., Clarke, 1962, 1980, 1983, 1986). These are chitinous hard structures, comparatively long-lasting in predator stomachs, capable of being identified up to the species level in many instances.

Incidentally, the collection of cephalopods from predator stomach contents provides valuable material for systematic and biological studies (e.g., Clarke, 1980; Bello, 1991).

The purpose of this paper is to point out the advancement in our knowledge of the pelagic cephalopod assemblage in the Adriatic Sea thanks to the study of the feeding habits of teuthophagous predators. As a matter of fact, a first study of the diet of swordfish from the Adriatic and adjacent seas (Bello, 1985 and 1991) was prompted by the need to assess the geographical distribution of pelagic cephalopods; *i.e.*, predators were used as collectors of otherwise elusive caphalopods.

A catalogue of the Adriatic cephalopods (Gamulin-Brida & Ilijanic, 1972) listed only 11 oceanic species out of 29 reported cephalopods (= 38%), whereas in the whole Mediterranean the occurrence of about 57 cephalopods has been recorded, 27 of which are oceanic (= 47%) (figures from several sources, including Mangold & Boletzky [1988] and Bello [1995b]). The difference between the two percentages is easily ascribable to the lack of proper investigations concerning the oceanic fraction of the cephalopod assemblage in the Adriatic (indeed, the benthic fraction was also poorly known; cf. Bello, 1990a).

A general description of the Adriatic and its teuthofauna is reported in Bello (1990a).

Materials and methods

The data referred in the Results section are based on information collected through the survey of the stomach contents of the following predators (in brackets the number of examined specimens):

- Risso's dolphin, *Grampus griseus* (Cuvier, 1812) (Cetacea: Delphinidae) [1]; (Bello, 1992b).
- Swordfish, *Xiphias gladius* Linnaeus, 1758 (Osteichthyes: Xiphiidae) [41]; (Bello, 1985, 1991, 1993, 1994, and unpublished data).
- Blue shark, *Prionace glauca* (Linnaeus, 1758) (Chondrichthyes: Carcharhinidae) [53]; (Politi, 1991; Bello, 1994).
- Smallspotted catshark, Scyliorhinus canicula (Linnaeus, 1758) (Chondrichthyes:

- Scyliorhinidae) [31]; (Bello, 1990a and 1995c).
- Blackmouth catshark, *Galeus melastomus* Rafinesque, 1810 (Chondrichthyes: Scyliorhinidae) [125]; (Bello, 1990a, 1995a, and 1995c).
- Velvet belly, *Etmopterus spinax* (Linnaeus, 1758) (Chondrichthyes: Squalidae) [128]; (Bello, 1990a, 1995c, and in press).

Swordfish, blue sharks, and Risso's dolphins are pelagic animals that capture most of their prey in midwater. Catsharks and velvet bellies are demersal selachians that prey upon both benthic and midwater organisms; it has been debated whether they are capable of moving a long distance away from the bottom (Relini-Orsi & Wurtz, 1975) or whether it is the midwater prey that periodically approaches the bottom and, hence, its predators (Macpherson, 1980) (see also Bello, 1995a and 1995c).

The Risso's Dolphin is strictly teuthophagous; the other predators display quite opportunistic feeding habits, although the swordfish appears to prefer cephalopods (Toll & Hess, 1981; Bello, 1991).

Results

The information deriving from the examination of teuthophagous predator stomach contents may be viewed from different angles.

The first level of interpretation shows the occurrence in the Adriatic of six oceanic cephalopods which had not been recorded by Gamulin-Brida & Ilijanic (1972) or earlier workers (cf. Bello [1990a] about Adriatic cephalopod records overlooked by Gamulin-Brida & Ilijanic [1972]) (Table 1). The newly recorded species are Heteroteuthis dispar, Abralia verany, Histioteuthis bonnellii, Ancistrocheirus lesueurii, Thysanoteuthis rhombus, and an unidentified cranchiid squid (one specimen of A. verany was also captured by bottom trawl [Guescini & Manfrin, 1986]).

However, when we check closely the list by Gamulin-Brida & Ilijanic (1972), we realize that most of the pelagic species reported therein were found only once (Onychoteuthis banksii, Ancistroteuthis lichtensteinii, Ommastrephes bartramii, Histioteuthis reversa, and Chiroteuthis veranii) or were otherwise considered to be rather rare (Todarodes sagittatus, Tremoctopus violaceus, and Ocythoe tuberculata). The occurrence of Brachioteuthis riisei in the Adriatic was indirectly asserted by Naef (1923) (report overlooked by Gamulin-Brida & Ilijanic [1972]). Furthermore, the specimen of Ch. veranii and, most probably, those of H. reversa and B. riisei were early juveniles caught by plankton net. The remaining pelagic species listed in Gamulin-Brida & Ilijanic (1972) are either infrequently collected (Argonauta argo) or very abundantly caught by bottom trawl and sold on the market (Illex coindetii and Todaropsis eblanae).

The data from predatorician studies offer a quite different picture (Tab. 1). Supposedly "rare" or "very rare" species, such as A. verany, O. banksii, A. lichtensteinii, T. sagittatus, and H. reversa, are indeed fairly common. Very common as well are H. dispar and H. bonnellii, previously unreported in the Adriatic Sea. In addition to the above mentioned cephalopods, the analysis of stomach contents showed the presence in the Adriatic of adult specimens of B. riisei and Ch. veranii; it also provided new finds of T. violaceus and O. tuberculata.

The overall picture of the oceanic cephalopod assemblage shows a couple of dominant species, namely *H. dispar* and *T. sagittatus*; three important elements, namely *H. bonnellii*, *H. reversa*, and *I. coindetii*; and a few comparatively common species, such as *A. verany*, *A. lichtesteinii*, and *O. banksii*. All other species appear to be preyed upon just occasionally.

In addition to the information on the presence and abundance of pelagic cephalopods in the

Adriatic Sea, data on the biology of some cephalopods were also gathered. For instance, it was shown that at nighttime *T. sagittatus* migrates towards the surface, where it is caught by swordfish; it was also shown that its population is composed by two age classes (0 + and 1 year) and that females grow faster than males (Bello, 1991).

Besides, some data were collected on the selectivity and preying mode of different predators. The swordfish is a powerful hunter that prefers muscular, fast swimming ommastrephid squids (Toll & Hess, 1981; Bello, 1991) and kills and maims its prey with its bill before ingesting it (Bello, 1994). The blue shark, on the contrary, is a very opportunistic feeder (Kohler & Stillwell, 1981) and contents itself with the ammoniacal histioteuthid squids (Bello, 1990b, 1994, and unpublished data; Politi, 1991). The blackmouth catshark appears to prefer morsel-size prey; *H. dispar* is by far the most preyed upon cephalopod (Relini-Orsi & Wurtz, 1975; Bello, 1995c; Sartor & De Ranieri, 1995). The velvet belly, in spite of its small size, attacks comparatively large prey items and most probably carries out group preying (Bello, 1995c and in press).

Discussion

The examination of the stomach contents of teuthophagous predators has greatly enhanced our knowledge of the Adriatic pelagic cephalopod assemblage. This type of study has shown both the occurrence of species previously unknown in the Adriatic, viz. Heteroteuthis dispar, Abralia verany, Histioteuthis bonnellii, Ancistrocheirus lesueurii, Thysanoteuthis rhombus, and Cranchiidae sp., and, most important, the abundance of several cephalopods, viz. H. dispar, A. verany, Onychoteuthis banksii, Ancistroteuthis lichtensteinii, Todarodes sagittatus, Histioteuthis bonnellii, and Histioteuthis reversa. The overall picture is one of comparatively great diversity and large biomass.

As already pointed out by Clarke (1966, 1977, 1980, 1983), many predators are efficient collectors of seemingly rare species. A question arises. How efficient in sampling are teuthivorous predators? The question may be put in a different way. How selective are cephalopod predators? Wormuth & Roper (1983) write "While our data from small nets suggest that cephalopods are low in abundance when viewed on a tow by tow basis, data from cephalopod predators suggest otherwise (CLARKE, 1977). In these two extremes we have a nonselective 'predator' and a very selective predator; both introduce opposite bias in their characterization of cephalopod abundance." Indeed, the picture of the Adriatic pelagic cephalopod assemblage offered in Results is strongly biased. For instance, no specimen of the actually abundant T. eblanae was found. Furthermore, just a quick look at Table 1 reveals the profound differences in the diets of different predators from the same habitat (compare with each other the prey item lists of swordfish, blue sharks and Risso's dolphin). This should warn as not to extrapolate the raw data from one or a few predators to figure out the composition of the assemblage of pelagic cephalopods. For example, according to the diet of the swordfish, by far the largest fraction of midwater cephalopod biomass in the South Adriatic and adjacent seas seems to be constituted by Todarodes sagittatus (Bello, 1990c); if other animals such as the Risso's dolphin and the blue shark are taken into account, one gets the idea that histioteuthid squids make up the bulk of the biomass; lastly, A. verany showed up only in the stomach contents of demersal selachians. Therefore, it is essential to use data from many specimens of many species of predators to get a more exact picture of the real situation.

Oceanic cephalopods play an important role in pelagic food webs of the South Adriatic as well as in the world ocean (AMARATUNGA, 1983). The feeding of the three largest predators

examined by the author –Risso's dolphin, swordfish, and blue shark– depends heavily upon cephalopods. These molluscs are capable of withstanding the heavy preying pressure thanks to their high growth rates and rapid turnover. As already reported (Bello, 1991), "Through them an efficient energy transfer occurs from bottom level consumers to large teuthivorous predators."

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- 	+	F			+	‡	ARGONAUTIDAE Argonauta argo Linnaeus, 1758
,		ı	+	,	+	‡	OCYTHOIDAE Ocythoe tuberculata Rafinesque, 1814
,				+	ı	‡	TREMOCTOPODIDAE Tremoctopus violaceus Delle Chiaje, 1830
							OCTOPODA
		,		+		•	CRANCHIIDAE sp.
,				ı	+	+	CHIROTEUTHIDAE Chiroteuthis veranii (Férussac, 1835)
1				+	•		THYSANOTEUTHIDAE Thysanoteuthis rhombus Troschel, 1857
	1					+ +	Todaropsis eblanae (Ball, 1841)
	ţ ·		+_‡	+ + + + + +	‡ ·	‡‡	Todarodes sagittatus (Lamarck, 1798) Iller coindetti (Vérany 1839)
	• :		1			+	OMMASTREPHIDAE Ommastrephes bartramii (Lesueur, 1821)
•	+		,	+	•	+	BRACHIOTEUTHIDAE Brachioteuthis riisei (Steenstrup, 1882)
‡+	+ +		‡ ‡ ‡ ‡ ‡ ‡	‡‡	‡‡	. +	HISTIOTEUTHIDAE Histioteuthis bonnellii (Férussac, 1835) Histioteuthis reversa (Vetrill, 1880)
				+ ‡	+ +	+ +	ONYCHOTEUTHIDAE Onychoteuthis banksii (Leach, 1817) Ancistroteuthis lichtensteinii (Férussac, 1839)
	•	ı	,	+	,		ANCISTROCHEIRIDAE Ancistrocheirus lesueurii (d'Orbigny,1842)
‡	+			,	,	,	ENOPLOTEUTHIDAE Abralia verany (Rüppell, 1844)
							TEUTHOIDEA
‡	† † †	‡		‡ ‡	‡		SEPIOLIDAE Heteroteuthis dispar (Rüppell, 1844)
							SEPIOLIOIDEA
E. spinax	G. melastomus	S. canicula	P. glauca	X. gladius	G. griseus	1972	



Figure 1 - Upper beak of an adult specimen of *Ommastrephes bartramii*; found in the stomach of a swordfish. Fig. 2 - Lower beak of a subadult specimen of *Histioteuthis bonnellii*; found in the stomach of a swordfish. Fig. 3 - Subadult specimen of *Onychoteuthis banksii* at an early digestion stage; found in the stomach of a swordfish. Note the lack of skin, suckers and hooks and the semidigested visceral organs (placed outside the mantle by the author)